Reconsideration of the inclusiveness of genus *Plasmophagus* (Chytridiomycota, *posteris traditus*) based on morphology

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ABSTRACT

Plasmophagus De Wildeman (1895), a presumably primitive fungal genus, has been considered to contain one or three species. Judging it to contain more than the original species (*P. oedogoniorum* De Wildeman, 1895), however, is a relatively recent taxonomic assessment. Dick (2001) recognized three species—placing genus *Plasmophagus*, though of uncertain position, in association with (but not necessarily included in) what one would interpret as the Oomycota (cf. "Peronosporomycotina" Dick). Our analysis of original (and other) literature and illustrations led to the realization that, as presently recognized (cf. Dick, 2001; *Index Fungorum*, as of this writing), *Plasmophagus* is a heterogeneous assemblage. Each of three supposed species apparently belongs to a different genus; two of these, including the original species, are in (probably closely related) genera, that may be considered (based on classical characters) to belong to Phylum Chytridiomycota, Kingdom Fungi; the third alleged species is best placed in a genus in Phylum Oomycota, Kingdom Straminipila (cf. "Chromista," some authors). *Plasmophagus* is consistent as a genus only in its initial, monotypic sense, and aligns (traditional classification) with Chytridiomycetes rather than Oomycetes. Molecular investigations could clarify the systematic placement of *Plasmophagus*, i.e., if it should possibly be in the Opisthosporidia/Cryptomycota (in which a potentially related genus, *Rozella*, has now been reclassified). Published on-line www.phytologia.org *Phytologia 98(2): 128-136 (Apr 4, 2016).* ISSN 030319430.

KEY WORDS: Chytrid, *Coleochaete*, *Draparnaldia*, host-cell, *Oedogonium*, Olpidiaceae, *Olpidiopsis*, *Olpidium*, Opisthosporidia, parasite, *Rozella*, Rozellopsidales, sporangium, *Tribonema*, zoospores.

In a comparatively recent taxonomic/nomenclatural treatment, Dick (2001, pp. 380-381) included genus *Plasmophagus* (*insertae sedis*, not assigned to a family; *sphalm.* Pseudosphaeritaceae, Beakes et al., 2014, p. 50) in his newly described Order Rozellopsidales (Order also *incertae sedis*). Though at first glance seemingly an "oomycetous grouping," Dick (2001) did not include Order Rozellopsidales within Class Peronosporomycetes (this Class roughly equivalent to a restrictive concept of the traditional Class, Oomycetes; see explanatory paragraph in Beakes et al., 2014, p. 52). More confusingly, Dick (2001, p. 274) apparently included his new Order (ostensibly containing *Plasmophagus*) within, but at the same time "provisionally excluded" it from, the broader grouping, Subphylum Peronosporomycotina (in "Phylum" Heterokonta, cf. p. 275). Subphylum Peronosporomycotina (described by Dick, 2001, p. 288) may be considered largely equivalent to Phylum Oomycota (cf. Beakes et al., 2014, p. 52). We note in passing that some workers (e.g., Petersen and Rosendahl, 2000) have employed "Peronosporomycetes" as a Class within Phylum Oomycota. Regardless, even in a wider survey of pertinent 21st century literature, no conclusive placement of genus *Plasmophagus* (*totus*) is evident.

For more than a century, *Plasmophagus* was monotypic, containing only the original species, *P. oedogoniorum* De Wildeman (1895). Without explanation, Dick (2001, p. 380-381) recognized three species in the genus: "*Plasmophagus oedogoniorum* É. de Wildeman," "*Plasmophagus deformans* (I. L. Serbinov) M. W. Dick," and "*Plasmophagus coleochaetis* (F. K. Sparrow, R. A. Paterson & R. M. Johns) M. W. Dick;" the last two alleged species of *Plasmophagus*, transferred from other genera, represent new combinations effected by Dick (2001). As regards authorship of *P. deformans*, we note that the spelling "Serbinov" (given by Dick) should be "Serbinow." Dick (2001) indicated that "*Rozella* sp. (Schulz, 1922)" represented an "unidentified species referable to *Plasmophagus*." By listing the Schulz reference

under "*Plasmophagus coloechaetis*," Dick (2001) may have been implying that a taxon in Schulz (1922) might be referable here (i.e., to *P. coleochaetis*). Our examination of the Schulz (1922) paper, however, revealed no organism definitely referable to *Plasmophagus*—and certainly not to "*Plasmophagus*" (*Rozella*) *coleochaetis*, since Schulz' 1922 article dealt with desmids (*Coleochaete*, not a desmid, was not found in this article). We also examined Schulz' 1923 paper—dealing primarily with parasites of desmids (and a member of the Zygnemataceae)—and likewise found no definitive match for *Plasmophagus*.

Based on traditional morphology, it appears that two of the species included by Dick (2001) under *Plasmophagus*—*P. oedogoniorum* (the "type") and *P. coleochaetis*—are members of the Chytridiomycetes (Chytridiomycota), cf. De Wildeman (1895), Fitzpatrick (1930), Sparrow (1960) and Karling (1977); accordingly, these two taxa would be considered to belong to Kingdom Fungi. However, the third species, *P. deformans*, has been deemed (statedly or implicitly) to have a placement within the Oomycetes (Oomycota), cf. Sparrow, 1943, 1960 and Karling, 1981; if so, this (third) taxon would presently be encompassed within Kingdom Straminipila (cf. Dick, 2001; or Kingdom Chromista, cf. Cavalier-Smith, 2001), not Kingdom Fungi (i.e., as now more restrictively recognized, cf. Blackwell and Powell, 1995; Cavalier-Smith, 2001). Attempting to properly sort out these points (and address associated nomenclatural questions) constituted the basis for undertaking the present investigation.

CLASSICAL TAXONOMIC HISTORY AND NOMENCLATURE OF *PLASMOPHAGUS*
(**Figs. 1-9:** Illustrations of Organisms and Structures Discussed)

The genus *Plasmophagus* was established in 1895 by De Wildeman on the basis of a single species, *P. oedogoniorum* (**Figs. 1-3**), found in *Oedogonium* sp. This parasite was also putatively found (**Fig. 4**) in *Tribonema bombycina* (Sparrow, 1933). *Plasmophagus* was placed in the chytridiaceous family, Olpidiaceae (cf. Fitzpatrick, 1930; Sparrow, 1960)—the simple, single-celled thallus in this family lacks the rhizoidal system ("vegetative structures") characteristic of a majority of Chytridiomycete families (cf. Sparrow, 1960, p. 120-122; Blackwell et al. 2006, p. 94, 97) and is holocarpic (entirely converting to a sporangium in asexual reproduction). At first amoeboid, the thallus of *Plamophagus* eventually more or less fills the algal host-cell (distinguishing it from genus *Olpidium*), allegedly becoming walled in the process; however, the "sporangial wall" (or containing membrane) of the parasite does not fuse (or completely fuse) with the host cell-wall—in supposed distinction to a similar genus, *Rozella*, also traditionally placed in the Olpidiaceae, in which such (complete) fusion is said to occur (Sparrow, 1960; Karling, 1977). Some hypertrophy of the host-cell is a consequence of infection by *Plasmophagus* (as in the case of infection by some species of *Rozella*). The small, posteriorly uniflagellate zoospores (longer than broad; with a single refractive globule) are released, laterally (though sometimes toward one end of the cell), through a modest discharge-pore; the discharge papilla is small, or obscure, barely penetrating the host-wall to the outside. Resting spores were not observed.

Five years after publication of Sparrow's second edition of *Aquatic Phycomycetes* (1960), Sparrow, Paterson and Johns (1965) published "Additions to the Phycomycete Flora of the Douglas Lake Region," Michigan. Included in Sparrow et al. (1965) was a description of a new species of *Rozella*, *R. coleochaetis* (**Fig. 5**), by Sparrow (*solum*). *Rozella*, though with more species, has been considered generally similar to *Plasmophagus* (cf. Sparrow, 1960; Karling, 1977). In both genera, the sporangium may essentially occupy the space within the host cell. In his key to genera of the traditional Chytridiomycete family, Olpidiaceae, Sparrow (1960) distinguished these genera by the fact that, in *Rozella*, the sporangial "wall" of the parasite (*Rozella*) and the host cell-wall supposedly become fused, with no space existing between them. In *Plasmophagus*, although the sporangium often comes to more or less fill the host-cell, fusion (or complete fusion) of the "walls" (parasite and host) is not attained. Regardless of the specifics of development (i.e., exactly "how it happens"), the morphological distinction (of *Rozella* and *Plasmophagus*) is that, in *Plasmophagus*, limited "space" between parasite and host may be visible in places (**Figs. 1, 3**). Concerning the species of *Rozella* (*R. coleochaetis*) found in "free-

filament portions" of the cushion-like green-alga *Coleochaete*, Sparrow (*in* Sparrow et al., 1965) concluded that complete fusion of host and parasite partitions must somehow take place, because, at maturity, their "walls" were "indistinguishable"—in other words, it wasn't possible (in a developed thallus) to tell where the boundary of the parasite ended, and the host began. Indeed, no separated "wall-areas" are evident in illustrations of *Rozella coleochaetis* Sparrow (Sparrow et al., 1965, figs. A-E), and one observes in these drawings only a unitary containing-structure (see also our **Fig. 5**). We find no basis, regarding the nature of "wall-fusion" or other traditional characters, for transfer of *Rozella coleochaetis* to genus *Plasmophagus*—viz. *P. coleochaetis* (Sparrow) Dick—as (questionably) effected by Dick (2001).

The posteriorly uniflagellate zoospores of *Rozella coleochaetis* suggest a chytridiomycetous (Fungal) classification for this taxon—not a placement within the Peronosporomycotina [Oomycota, Straminipila], which would seem at first glance to have been indicated by Dick (2001, p. 380-381) in his "circumscription" of *Plasmophagus* (this including *R. coleochaetis*, as *Plasmophagus coleochaetis*). As mentioned, though, Dick (see his pp. 274, 371) left the "relationship" of Order Rozellopsidales (to which genus *Plasmophagus* was assigned by him) "*insertae sedis;*" not only was the Order *not* included in the Peronosporomycetes, it was "provisionally excluded" from the broader grouping, Peronosporomycotina. Dick (2001) did not indicate where Order Rozellopsidales should be placed; in a footnote (p. 254) Dick noted that this Order contained both uniflagellate and biflagellate taxa [encompassing, thus, possibly unrelated organisms]. Beakes et al. (2014, p. 52) noted there had been additional molecular insights since Dick's (2001) compilation, raising questions about certain higher level taxa recognized by Dick, and suggesting the need for additional resolution of less-studied Orders [such as the Rozellopsidales]. In further uncertainty, *Plasmophagus* (including *Rozella coleochaetis*, according to Dick) was indicated as *insertae sedis* within the Order Rozellopsidales. In any event, as for possible actual placement of *Rozella coleochaetis*, not only are its zoospores posteriorly uniflagellate (consistent with chytrid zoospores), but the somewhat elongate, generally straight, form of these small spores compares well with zoospore-form of other species of *Rozella*—e.g., *R. allomycis* and *R. polyphagi*—*Rozella* being historically classified in the Olpidiaceae/Chytridiomycetes (cf. Sparrow, 1960). The initial taxonomic assignment of *R. coleochaetis* to *Rozella* (and to Chytridiomycota, *a maioribus traditus*) by Sparrow (Sparrow et al., 1965), seems to be supported by "thallus-fusion with the host-cell" (paragraph above) *and* zoospore morphology. Again, we find no substantive basis for Dick's (2001) transfer of *R. coleochaetis* to *Plasmophagus*.

Even if one were to accept Dick's (2001) unexplained transfer of *Rozella coleochaetis* to *Plasmophagus*, matters of nomenclatural concern remain. Dick credited publication of *Rozella coleochaetis* to "F. K. Sparrow, R. A. Paterson & R. M. Johns" (authors of the 1965 paper; cf. Sparrow et al., 1965, above). However, Sparrow *alone* is author of this species—*in* Sparrow, Paterson & Johns (1965)—and the specific epithet ("*coleochaetis*") should be attributed only to Sparrow. *Index Fungorum* (IF), an online resource for fungal names, indeed recognized authorship as just "Sparrow," but listed the spelling of the epithet (under *Plasmophagus*) as *P.* "*coleochaetes*" (Sparrow) M. W. Dick (2001), rather than *P.* "*coleochaetis*." One might suspect perhaps that this spelling ("*coleochaetes*") of the epithet in IF would be based on the way Sparrow (*in* Sparrow et al., 1965) was thought to have originally spelled the name (*sic*, "*Rozella coleochaetes*," IF). However, Sparrow (in 1965) in fact spelled the original epithet "*coleochaetis*," not "*coleochaetes*." Dick (2001) simply utilized Sparrow's original spelling ("*coleochaetis*") in his (otherwise questionable) transfer to *Plasmophagus*.

As mentioned, Dick (2001) included three species in *Plasmophagus*, two species in addition to the chytridiaceous, "type" species (*P. oedogoniorum* De Wildeman, 1895). Of the additional two species included (transferred in) by Dick, *P. coleochaetis* (as discussed) seems best assigned to *Rozella* (Chytridiomycetes *sensu lato*); but, the other species, *Plasmophagus deformans* (Serbinow) Dick, is of questionable relationship. *Plasmophagus deformans* was based on a taxon, with biflagellate zoospores, described by Serbinow (1907, p. 153-154) under the name "*Pseudolpidium* (?) *deformans*" [later considered to belong to genus *Olpidiopsis*]. This organism is parasitic in lateral branches of the alga,

Draparnaldia (**Fig. 6**), in which it causes cell-hypertrophy. Though *P. deformans* (**Figs. 7-9**) was viewed as chytridiaceous by Serbinow, the critical distinction between posteriorly-uniflagellate forms (probable Chytridiomycetes) and biflagellate (often laterally biflagellate) forms—these "biflagellates" turning out *not* to be chytrids—was not necessarily clear in 1907, and developed over a period of years (cf. Scherffel, 1926; Sparrow, 1943). Sparrow (1943, 1960) placed genus *Pseudolpidium* in the Olpidiopsidaceae of the Lagenidiales—these being Oomycetes, *not* Chytridiomycetes. Sparrow (1943, p. 609) questioned the status of some species of *Pseudolpidium*, yet recognized the genus *pro parte* (pp. 636-638); he listed *P. deformans* as an "imperfectly known" species under this genus, and did not include it in the key to species. Later, Sparrow (1960, p. 955), still (questioningly) recognizing *Pseudolpidium*—referring to the genus as "a dumping ground" for several incompletely known species—included *P. deformans* in the genus (this time, including it in his species key). Karling (1981) transferred *Pseudolpidium deformans* to *Olpidiopsis* (also a genus of Oomycota)—viz., *Olpidiopsis deformans* (Serbinow) Karling—*not* to *Olpidium*. Sparrow (1960) considered the two flagella of zoospores of *Olpidiopsis deformans* (i.e., *Pseudopidium deformans*, cf. Sparrow, 1960) to be laterally inserted; Karling (1981) thought them possibly laterally inserted, but added a question mark (and did not illustrate them as lateral; his plate 5, fig. 184). Regarding illustrations of "*P. deformans*," Serbinow's (1907) figure 28 (of Plate III/IV) shows the biflagellate nature of the zoospores, and that the insertion of the two, possibly unequal flagella is perhaps apical or sub-apical (**Fig. 9**). In any case, the biflagellate character of the zoospores indicates that they are *not* chytridiaceous (i.e., not fungal) zoospores, and would support a placement of "*Olpidiopsis deformans*" (i.e., *Plasmophagus deformans*, cf. Dick, 2001; i.e., *Pseudolpidium deformans*, cf. Serbinow, 1907; Sparrow, 1960) within the Oomycota (and hence within Kingdom Straminipila).

Thus, although Dick (2001)—in what is apparently the most recent taxonomic treatment of the genus—included genus *Plasmophagus* in an Order (Rozellopsidales) of uncertain position (and *Plasmophagus* was not assigned by Dick to a family within this Order), he nonetheless loosely associated this Order (and genus) with Peronosporomycotina (i.e., Oomycota). However, whereas Dick included three species under *Plasmophagus*, only one of these (*P. deformans*) is referable to a genus of Oomycota. The other two species included by Dick (*P. oedogoniorum* and *P. coleochaetis*)—though in different (perhaps closely related) genera—are better referred, based on traditional morphology and classification, to the Chytridiomycota. Since the "type species," *P. oedogoniorum*, is determinable as a Chytridiomycete (*praeteritum tempus*), *Plasmophagus* should not be considered an Oomycete genus—and Dick's "provisional exclusion" of the Order containing this genus from the Peronosporomycotina, though he provided no reason for this, would (in so far as his tentative statement went) be upheld.

SUMMARY OF TRADITIONAL SYSTEMATIC INFORMATION

Genus *Plasmophagus* as recognized by Dick (2001), though "encompassing" only three species (*P. oedogoniorum*, *P. coleochaetis*, and *P. deformans*), is a disparate assemblage. Each species, in fact, probably represents a different genus—one of these (*P. deformans*) being unrelated to the other two.

Plasmophagus (De Wildeman, 1895) initially contained a single species (*P. oedogoniorum*) and seemingly fitted well in the simple-structured, presumably primitive Chytridiomycete family, Olpidiaceae (cf., Fitzpatrick, 1930; Sparrow, 1960; and Karling, 1977, provisionally). *Plasmophagus* (*sensu originalis*) has been distinguished (Sparrow, 1960) from *Olpidium* (i.e., *Olpidium* as traditionally understood) by a sporangium which virtually fills the host-cell, and from *Rozella* by the fact that the "sporangial wall" does not (uniformly) "fuse" with the host cell-wall.

Sparrow's (*in* Sparrow et al., 1965, pp. 117-118) description of *Rozella coleochaetis* should have had little effect on the taxonomy of genus *Plasmophagus*. Sparrow pointed out that, whereas *Rozella coleochaetis* resembled *Plasmophagus oedogoniorum*, *R. coleochaetis* differed "in having complete fusion of host and parasite wall." Though *Rozella* and *Plasmophagus* were similar, they were recognized

as distinct genera (cf. Sparrow, 1960) based on alleged degree of "wall-fusion." In any case, Dick (2001) provided no rationale for his transfer of *Rozella coleochaetis* Sparrow to *Plasmophagus*. Based on Sparrow's (1965) original description and illustrations, *R. coleochaetis* should remain in *Rozella* (as it has been classically recognized, by morphological characteristics). *Rozella*, traditionally recognized as a Chytridiomycete genus, may actually place in a related grouping (or "clade"), as will be discussed.

The third alleged species of *Plasmophagus*, *P. deformans* (Serbinow) Dick (2001), has been the most difficult to determine. This species is apparently not a Chytridiomycete, and not even in Kingdom Fungi. It should, rather, be included with those organisms recognized as Oomycetes [Oomycota], cf. Sparrow (1960) and Karling (1981), these encompassed within Kingdom Straminipila (Dick, 2001; or Kingdom "Chromista," if one prefers a broader kingdom concept, cf. Cavalier-Smith, 2001; Blackwell, 2009). The further placement of "*P. deformans*" seems best at present in genus *Olpidiopsis* (Oomycetes), see Karling (1981), *not Olpidium*. We cannot agree with Dick's (2001) transfer of *Olpidiopsis deformans* to *Plasmophagus* (since *Plasmophagus* was founded as a chytridiaceous genus).

In summary of traditional information, *Plasmophagus*, as recognized by Dick (2001) and enumerated in *Index Fungorum* (presently), is polymorphic, containing: (1) one chytrid-like, original species, in Kingdom Fungi; (2) a second, initially "chytrid" species which belongs to a similar, possibly related, fungal genus, *Rozella*; and (3), a third, "oomycete" species which apparently belongs to a fundamentally different genus, *Olpidiopsis* (not *Olpidium*), this in a different kingdom (Straminipila, not Fungi). If *Plasmophagus* is to be definably recognized, it should (based on traditional taxonomic characters, and in the absence of molecular data) be returned to its initial, monotypic status (containing only *P. oedogoniorum*). Though classically considered to be a chytrid, it remains to be seen if *P. oedogoniorum* will ultimately place within the Chytridiomycota, or in a related group of organisms (if certain molecular information can be obtained).

CURRENT STATUS OF CLASSIFICATION

Although *Plasmophagus* and *Rozella* were earlier classified as members of the Olpidiaceae (Sparrow, 1960), in the Chytridiales, Barr (1980) transferred *Rozella* to a newly erected order, Spizellomycetales. However, molecular phylogenetic analysis has revealed that *Rozella* as well as *Olpidium* place in lineages outside of the Chytridiomycetes (James et al. 2006). *Olpidium* (at least certain species) is in a lineage that diverges among zygomycetous fungi. *Rozella* is now classified (based in particular on molecular study of *R. allomycis*) in a clade, sister to the traditionally recognized Kingdom Fungi, which Karpov et al. (2014) circumscribed as Superphylum Opisthosporidia—*Rozella* is classified in Phylum Cryptomycota within this superphylum (Opisthosporidia). Determining the molecular comparison of *R. coleochaetis* to, for example, *R. allomycis*, will prove essential for final confirmation of the placement of *R. coleochaetis* in genus *Rozella*.

Additional information has also come from transmission electron microscopy, especially as regards modified understandings of the host-parasite interfaces of two species of *Rozella* (Held, 1981; Powell, 1984). Rather than forming its own sporangial wall during the vegetative stage, as earlier interpreted (e.g., Sparrow, 1938, 1960; Karling, 1977), *R. allomycis* (Held, 1981) and *R. euglenae* (Powell, 1984) were found to develop as endoplasmodial parasites which make direct contact with host cytoplasm. It appears that this endoplasmodial stage of *Rozella* phagocytizes the host protoplasm (Powell, 1984) and ultimately enlarges until it totally fills the host compartment—and that this parasite does not develop its own wall but uses the host wall (as a containing vessel) as it cleaves its zoospores (Held, 1981); these posteriorly uniflagellate zoospores are subsequently typically discharged, to the exterior of the host, by a pore generated in the host cell-wall.

If *Plasmophagus* is related to *Rozella* (as implied; cf. Sparrow, 1960), *Plasmophagus* may also ultimately place phylogenetically outside of the Chytridiomycetes, and among the Opisthosporidia. Supporting this possibility, *Nucleophaga amoebae*—traditionally classified in the Olpidiaceae, and an organism considered possibly related to both *Rozella* and *Plasmophagus*—has recently been revealed as a member of the Opisthosporidia clade (Corsaro et al., 2014). However, the phylogenetic affinity of *Plasmophagus* can only be definitively determined by collecting it and sequencing its genes, an intriguing challenge. For the time being, *Plasmophagus* remains recognized as a member of the Chytridiomycetes.

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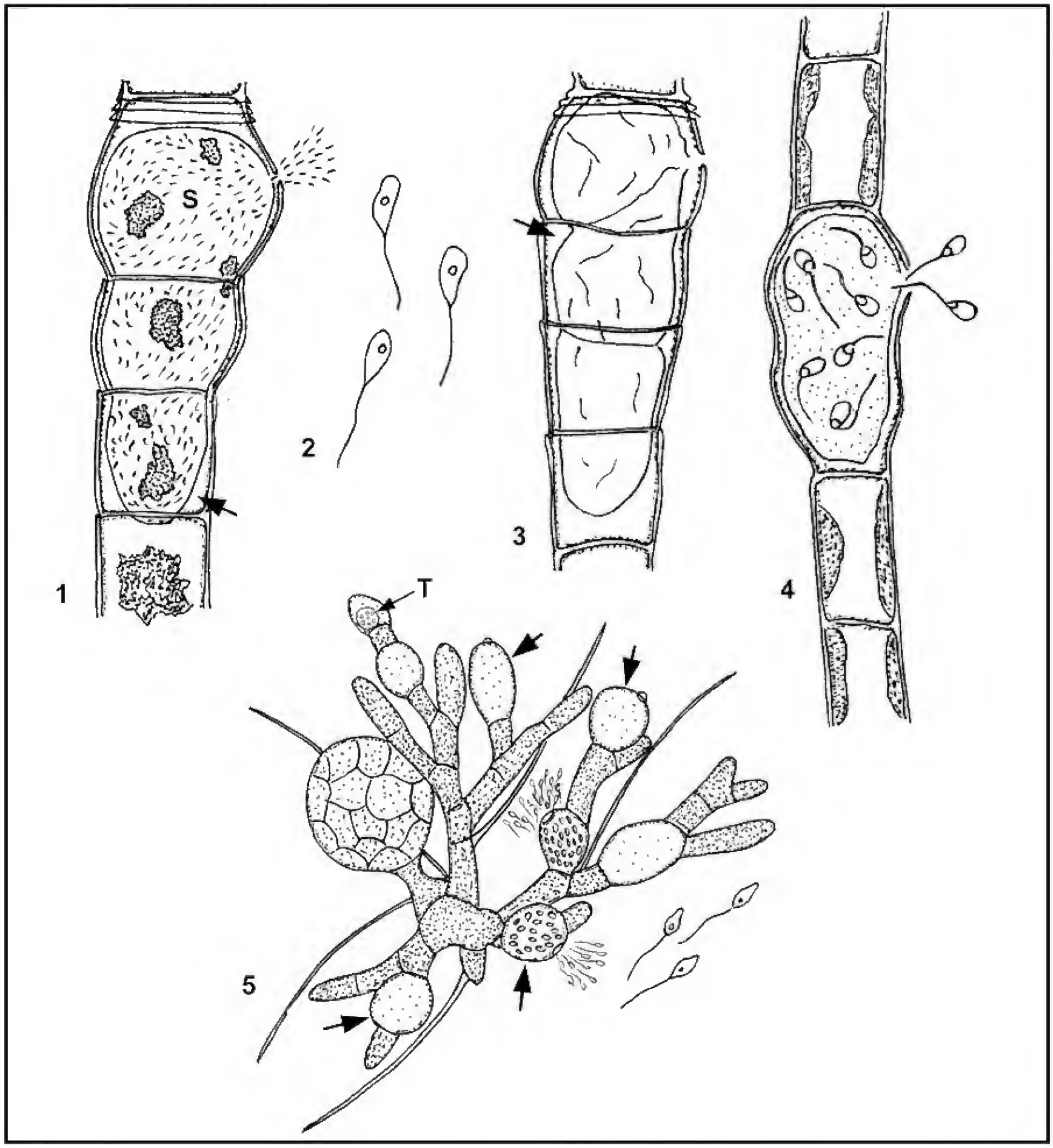

Figs. 1-4: *Plasmophagus oedogoniorum.* Fig. 1: Sporangia of *P. oedogoniorum* parasitic in successive *Oedogonium* cells; sporangium (S) mostly fills algal cell, but "free space" evident in places (arrow); note small zoospores, released from lateral pore in uppermost cell. Fig. 2: Elongate form of the posteriorly uniflagellate zoospores. Fig. 3: Older, empty sporangia; "space" between parasite and *Oedogonium*-host more evident at this stage (arrow). Fig. 4: Putative *P. oedogoniorum* in alga, *Tribonema*; note zoospore release from lateral pore. **Fig. 5**: Sporangia of *Rozella coleochaetis* (arrows), each completely filling a cell of the algal host (*Coleochaete)*, no "free space" evident*;* note small, elongate zoospores (generally similar to those of *Plasmophagus*) released from two sporangia (mid-, lower-right); *R. coleochaetis* young thallus (T) -- Figs. 1-3 after De Wildeman, 1895; Fig. 4 modified from Sparrow 1933; Fig. 5 modified from Sparrow et al., 1965.

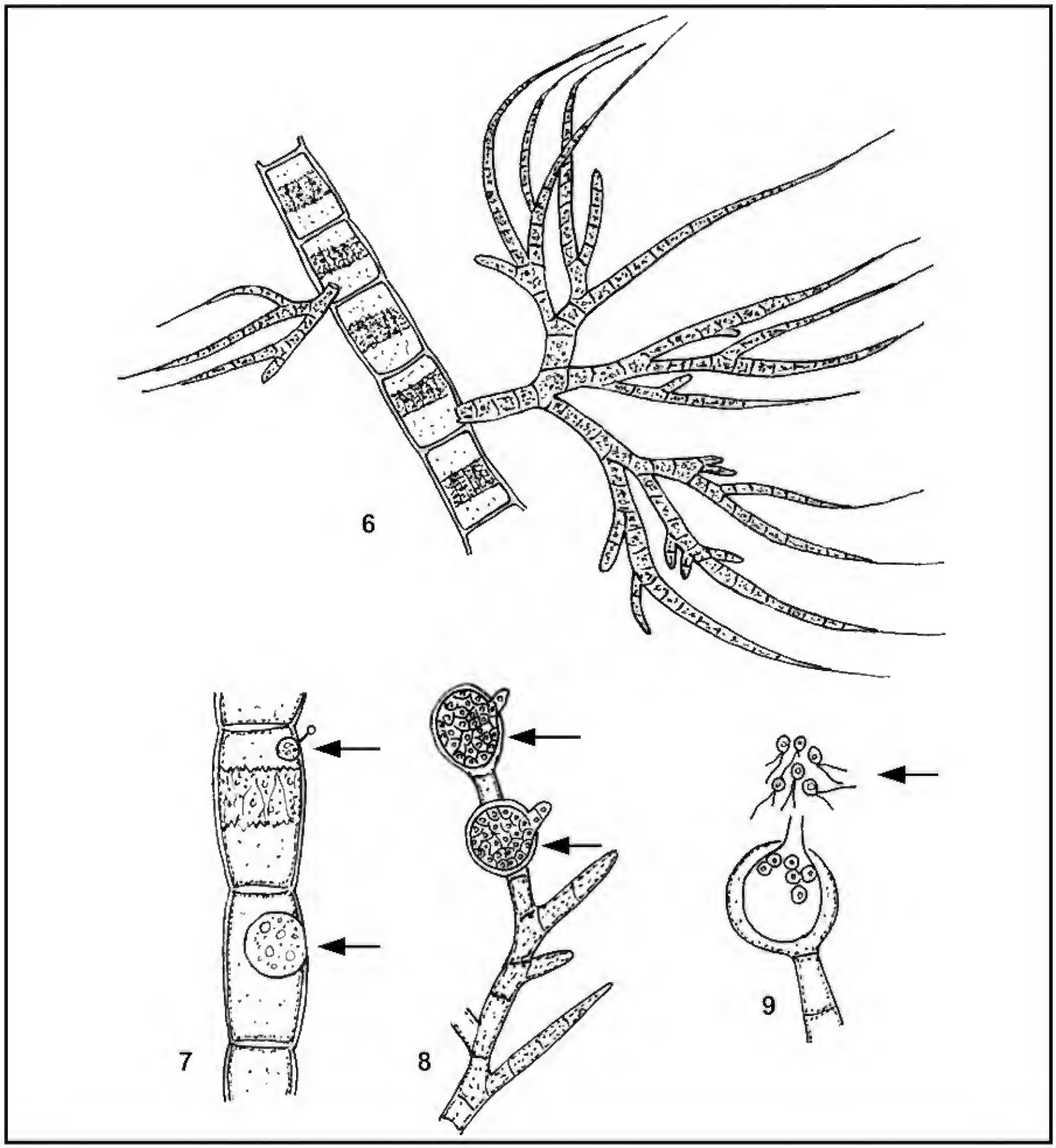

Fig. 6: *Draparnaldia*, the algal host for *Pseudolpidium deformans* ("*Plasmophagus*" *deformans*, Dick, 2001); note the main, algal axis and smaller diameter, tip-pointed, lateral branches (cells of these lateral branches are potential sites of infection by *P. deformans*). **Figs. 7-9**: *Pseudolpidium deformans* (= *Olpidiopsis deformans*, Karling, 1981). Fig. 7: Infection of two cells of *Draparnaldia* lateral filament (arrows); upper algal-cell shows slender zoospore-germ-tube still present; cell below shows young, endobiotic sporangium. Fig. 8: Developed sporangia (arrows) of *P. deformans*, zoospores not yet released. Fig. 9: Release of zoospores from mature sporangium, the zoospores developing motility; zoospores (arrow) are biflagellate; note that the two, possibly unequal flagella of each zoospore are apparently apically or sub-apically inserted. -- Figs. 7-9 based on Serbinow, 1907.